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# **Stable isotopic composition of deep sea gorgonian corals (*Primnoa* spp.): a new archive of surface processes**

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## ABSTRACT

The deep-sea gorgonian coral *Primnoa* spp. lives in the Atlantic and Pacific Oceans at depths of 65-3200 m. This coral has an arborescent growth form with a skeletal axis composed of annual rings made from calcite and gorgonin. It has a lifespan of at least several hundred years. It has been suggested that isotopic profiles from the gorgonin fraction of the skeleton could be used to reconstruct long-term, annual-scale variations in surface productivity. We tested assumptions about the trophic level, intra-colony isotopic reproducibility, and preservation of isotopic signatures in a suite of modern and fossil specimens. Measurements of gorgonin  $\Delta^{14}\text{C}$  and  $\delta^{15}\text{N}$  indicate that *Primnoa* spp. feed mainly on zooplankton and/or sinking particulate organic matter ( $\text{POM}_{\text{SINK}}$ ), and not on suspended POM ( $\text{POM}_{\text{SUSP}}$ ) or dissolved organic carbon (DOC). Gorgonin  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in specimens from NE Pacific shelf waters, NW Atlantic slope waters, the Sea of Japan, and a South Pacific (Southern Ocean sector) seamount were strongly correlated with Levitus 1994 surface apparent oxygen utilization (AOU; the best available measure of surface productivity), demonstrating coupling between skeletal isotopic ratios and biophysical processes in surface water. Time-series isotopic profiles from different sections along the same colony were identical for  $\delta^{13}\text{C}$ , while  $\delta^{15}\text{N}$  profiles became more dissimilar with increasing separation along the colony axis. Similarity in C:N,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  between modern and fossil specimens suggest that isotopic signatures are preserved over millennial timescales. Finally, the utility of this new archive was demonstrated by reconstruction of 20<sup>th</sup> century bomb radiocarbon.

**Keywords:** *Primnoa*, gorgonin,  $\Delta^{14}\text{C}$ ,  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , trophic level, paleoceanography

**Running Head:** Surface processes recorded in deep sea gorgonians

## INTRODUCTION

*Primnoa resedaeformis* (Gunnerson) is a deep-sea gorgonian coral with known occurrences in North Atlantic, Arctic and North Pacific waters at depths of 65-3200 m (Breeze et al. 1997, Etnoyer & Morgan 2003). A subspecies, *Primnoa resedaeformis notialis* (Bayer), occurs on seamounts in the Southern Ocean sector of the Pacific Ocean. *Primnoa willeyi* (Hickson) and *Primnoa pacifica* (Kinoshita) are found in the eastern and western North Pacific, respectively (Smithsonian holdings:

<http://goode.si.edu/webnew/pages/nmnh/iz/Query.php>). These corals have an arborescent growth pattern with a skeleton made of calcite and a proteinaceous material called gorgonin (Goldberg 1976) arranged in alternating concentric rings around longitudinal growth axes (Risk et al. 2002, Sherwood 2002). Towards the outer growth surface of older portions of the skeleton the outer cortex may be comprised of just calcite, with gorgonin layers lacking. Based on  $^{14}\text{C}$  and Pb-Ra dating, visible layers in both the massive outer calcite cortex and calcite-gorgonin couplets towards the center of the skeleton appear to be annual in timing (Risk et al. 2002, Andrews et al. 2002). Sub-annual banding patterns have also been identified using scanning electron microscopy and Nomarski differential interference imaging (Risk et al. 2002, Sherwood 2002). This coral appears to have lifespans on timescales of up to several centuries (Andrews et al. 2002; Risk et al. 2002; Scott et al. 2005).

Based on  $^{14}\text{C}$  analyses, Griffin and Druffel (1989) originally suggested that the main source of carbon to deep-sea corals was sinking particulate organic matter (POM). They further suggested (Druffel et al. 1995) that the carbon and nitrogen isotopic composition of the proteinaceous layers of the colonial zoanthid *Gerardia* spp. could be a

recorder of surface ocean processes (productivity, nutrient sources, etc.). *Primnoa* spp. may also form its gorgonin skeleton from sinking POM, since  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  in the polyps and gorgonin show similar regional differences to  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  of surface water POM (Heikoop et al. 1998, 2002). Moreover, the  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  of the polyps is highly correlated to the  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  of associated gorgonin (Heikoop et al. 2002). Together, these results suggest that the isotopic composition of annual gorgonin layers could record the temporal history of processes that control the isotopic composition of POM (Heikoop et al. 2002) including plankton productivity and the  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  of nutrient sources (e.g. Ward-Paige et al. in press). The  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  of gorgonin from a suite of corals from Alaskan waters, waters off the eastern shore board of the United States and Canada, and a South Pacific seamount were positively correlated (Heikoop et al. 2002), suggesting that surface ocean productivity relative to nutrient supply may be the primary control on the isotopic composition of gorgonin.

For stable isotopic profiles generated from the annual gorgonin layers of *Primnoa* spp. skeletons to have any meaningful environmental significance, four conditions must be met: (1) the trophic position of *Primnoa* spp. must be known; (2) organic diagenesis must not affect the isotopic composition of the skeleton; isotopic trends must be reproducible among (3) different sections of the same colony; and (4) different colonies inhabiting the same area. The purpose of this paper is to test the first three of these assumptions using a suite of recently collected live and fossil specimens from the Atlantic and Pacific oceans. The fourth assumption will be the focus of a forthcoming study also dealing with skeletal chronology.

## MATERIALS AND METHODS

Specimens were obtained during research and fishing expeditions (Table 1). Seven additional specimens were obtained from the Smithsonian Institution National Museum of Natural History. *Primnoa resedaeformis* (Gunnerus) was collected from the NE Channel, southwest of Halifax, Nova Scotia (Fig. 1) and from east of Virginia Beach, USA. *Primnoa willeyi* (Hickson) was collected east of the Queen Charlotte Islands, Chatham Sound and Knight Inlet, British Columbia, and from the Aleutian Islands and Prince William Sound, Alaska. *Primnoa pacifica* (Kinoshita) was collected in the Sea of Japan. The subspecies *Primnoa resedaeformis notialis* was collected from a seamount in the Southern Ocean sector of the South Pacific. Three of the Smithsonian samples were originally reported in Heikoop et al. (2002); these are included here to highlight geographic trends in stable isotopic composition.

All specimens were collected alive, except for Fossil-95 and COHPS-2001-1. These dead-collected specimens were dated radiometrically by B. Ghaleb at GEOTOP-UQAM-McGill, Montreal, Canada (Scott et al. 2005). Samples from COHPS-2001-1 are ca. 150 yrs old, based on  $^{210}\text{Pb}$ - $^{226}\text{Ra}$  analyses of the outer calcite cortex region of the coral. Fossil-95 is ca. 2000 years old, based on two uranium-series dates on the middle and outer regions of a section of the colony.

Colonies for stable isotopic analyses (Fig. 2) were sectioned with a rock saw and ground and polished on a diamond lap wheel to a thickness of about 5 mm. Sections were photographed with a Nikon Coolpix digital camera in macro mode. After some trial and error we found that photographing the sections in ultraviolet light gave the clearest image

of ring patterns in the horny axis owing to contrast between the calcite-rich (luminescent) and gorgonin-rich (non-luminescent) portions of the annual growth rings (Fig. 3).

Annual gorgonin rings were isolated by dissolving sections in 5% HCl for a week (up to three weeks for larger sections). Upon dissolution sections were transferred to a Petrie dish filled with distilled water, and the annual rings were picked apart with tweezers and scalpel under a binocular microscope. Photographs of the sections taken before dissolution were used to guide sampling. Individual rings were placed in 5 ml polyethylene vials with 5 % HCl, for an additional week, to ensure that all the calcite had dissolved. After two more rinses in HCl, the rings were triple rinsed in de-ionized water and dried in a low temperature oven. Rings averaged about 5 mg in weight. Tissue material scraped off the skeletal axes was prepared in the same way.

Isotopic and C:N analyses of gorgonin were performed by Elemental Analyzer/Continuous Flow Isotope Ratio Mass Spectrometry at GEOTOP-UQAM-McGill. Isotope ratios are reported in conventional delta notation, where (example for carbon):  $\delta^{13}\text{C} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$ ; and  $R = {}^{13}\text{C}/{}^{12}\text{C}$ . Standards used were PDB ( $\delta^{13}\text{C}$ ) and air ( $\delta^{15}\text{N}$ ). Analytical error, as measured by the standard deviation of duplicate measurements, averaged 0.10 ‰ for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , and 0.01 for C:N. Some of the corals obtained from the Smithsonian Institute were preserved in ethanol, which may have affected stable isotopic compositions (Bosley & Wainright 1999).

Ten of the annual layers isolated from specimen DFO-2002-con5 (section A1) were analyzed for  $^{14}\text{C}$  by accelerator mass spectrometry at Lawrence Livermore National Laboratory following standard procedures.



Suspended particulate organic matter (POM<sub>SUSP</sub>) in the Gulf of Maine/Georges Bank region (Fig.1) was sampled as part of the Ecosystems Monitoring Survey at the Northeast Fisheries Science Center, Narragansett, RI, USA. Samples were collected in spring, summer and autumn, between November 2000 and August 2003. In addition, a vertical transect (depths 3.7 m, 100 m and 215 m) was sampled in the NE Channel in August 2004 (Fig. 1). Surface samples were obtained with a ship-board, near surface flow-through system. Deeper samples were collected with Niskin bottles attached to a CTD rosette. A volume of 600-1000 ml of water was pre-filtered through 300  $\mu$ m mesh to remove most zooplankton, then onto a GF/F filter. Samples were immediately frozen and transported to the US Environmental Protection Agency, Atlantic Ecology Division, Narragansett, RI for isotopic analysis. Nitrogen and carbon isotopic composition was determined by continuous flow isotope ratio mass spectrometry using a Carlo-Erba NA 1500 Series II Elemental Analyzer interfaced to a GV Instruments Optima Mass Spectrometer. All samples were analyzed in duplicate with a typical difference of about 0.1 ‰. Sample material was re-analyzed periodically over a several month period and exhibited a precision of 0.30 ‰, calculated as a single sigma standard deviation of all replicate values. This latter estimate of precision is appropriate for POM<sub>SUSP</sub>  $\delta^{15}\text{N}$  values determined in this study.

## **RESULTS**

### **Composition of tissue and skeletal gorgonin**

Stable isotope and C:N data for *Primnoa* spp. are summarized in Table 2. Missing entries reflect cases of insufficient sample material for analyses. There were large

differences in the isotopic and elemental composition between tissue and gorgonin. C:N ratios were higher and more variable in tissue (6.1 +/- 1.4, n = 11) than gorgonin (3.3 +/- 0.1, n = 8).  $\delta^{13}\text{C}$  values were more negative in the tissue by an average of 3.0 +/- 1.7 ‰ (n = 9). Most of this difference in  $\delta^{13}\text{C}$  may be accounted for by the difference in lipid content of the two fractions. Taking C:N as a proxy for lipid content, lipid-normalized values of  $\delta^{13}\text{C}$  ( $\delta^{13}\text{C}'$ ) were calculated from equations in McConnaughey & McRoy (1979). After normalization,  $\delta^{13}\text{C}'$  values were more negative in the tissue by 1.0 +/- 0.6 ‰ (n = 6). Values of  $\delta^{15}\text{N}$  were more positive in the tissue by 0.9 +/- 0.9 ‰ (n = 6).

The reason for lower  $\delta^{13}\text{C}'$  (even after lipid-normalization) and higher  $\delta^{15}\text{N}$  in the tissue compared with the gorgonin is not clear, but may be related to differences in tissue turn-over time (Tieszen et al. 1983). Each gorgonin layer integrates seasonal variations over one year, and the average isotopic compositions listed in Table 2 integrate inter-annual variations over many years. We expect that the tissue, which turns over in something less than one year, represents a unique seasonal signature. Another possibility relates to differences in the amino acid contents of the two fractions (O.A. Sherwood, unpublished data). Different amino acids are known to have unique and widely variable  $\delta^{13}\text{C}$  (Keil & Fogel 2001) and  $\delta^{15}\text{N}$  (McClelland & Montoya 2002); therefore, the relative proportion of amino acids between tissue and gorgonin may impart differences in stable isotopic content.

### **Geographic and interspecific variability**

There were significant compositional differences among the different species and geographic areas (Table 2). *Primnoa pacifica* and *Primnoa resedaeformis notialis* from

the Sea of Japan and South Pacific had the lowest tissue C:N values ( $4.5 \pm 0.4$ ,  $n = 3$ ). *Primnoa willeyi* from the NE Pacific had intermediate C:N ( $6.1 \pm 1.4$ ,  $n = 5$ ), and *Primnoa resedaeformis* from the NW Atlantic had the highest C:N ( $7.5 \pm 0.2$ ,  $n = 3$ ).  $\delta^{13}\text{C}'$  and  $\delta^{15}\text{N}$  were positively correlated ( $p < 0.001$ ; Fig. 4a), as previously found in Heikoop et al. (2002). Isotope values in  $\delta^{15}\text{N}$  vs.  $\delta^{13}\text{C}'$  space were clearly delineated by geography, with highest values in the NE Pacific, intermediate values in the NW Atlantic and Sea of Japan, and lowest values in the Pacific-Southern Ocean Sector (Fig. 4a). The sample from Atka Island in the NE Pacific (Smith-1010257) deviated from this pattern; it had isotopic values more similar to the South Pacific samples.

Isotope values were plotted against apparent oxygen utilization (AOU), selected from the Levitus and Boyer (1994) dataset as the best available measure of surface productivity for open ocean, slope water and shelf sites alike (Fig. 4b). Surface-water AOU data were obtained from the  $0.5^\circ$  latitude X  $0.5^\circ$  longitude grid nearest each of the coral collection locations. Both  $\delta^{13}\text{C}'$  and  $\delta^{15}\text{N}$  significantly increased with more negative AOU (i.e. higher productivity;  $p < 0.0001$ ).

### **Intra-colony isotopic reproducibility**

Specimen HUD2001-055-VG15 was the first colony examined for trends in the isotopic composition of annual gorgonin rings. This colony was collected alive and transferred to an aquarium, where the tissue layer eventually died and sloughed off the skeleton. A 50 cm long main branch was snapped off the colony for geochemical sampling. Sections for stable isotopic analyses were cut from the base of the main branch, and from two divergent branches 10 cm higher up the colony (Fig. 2a). The basal section

measured 14 mm in diameter. Stable isotope and C:N profiles from this specimen are shown in Fig. 5. The  $\delta^{13}\text{C}$  profiles were identical among the three different sections (correlation coefficients ( $r$ ) ranged 0.84 to 0.97;  $p < 0.0001$ ), showing trends towards heavier values with increasing age. The amplitude of  $\delta^{13}\text{C}$  profiles was 3 ‰, much larger than the analytical error (0.10 ‰).  $\delta^{15}\text{N}$  profiles were less reproducible between the different sections ( $r = 0.38$  to  $0.48$ ;  $p = < .01$  to  $.05$ ). Differences among coeval rings, up to 1.5 ‰, were equivalent to the amplitude of the profiles, and cannot be explained by analytical error. C:N profiles were the least reproducible among the different sections ( $r = -0.23$  to  $0.44$ ;  $p = 0.02$  to  $0.78$ ), with differences among coeval rings (up to 0.07) exceeding the analytical error (0.01).

A larger colony of *Primnoa resedaeformis* (DFO-2002-con5) was subsequently obtained from the Canadian Department of Fisheries and Oceans and the same experiment was repeated. This colony was completely covered in live tissue and was frozen immediately after collection (Fig. 2b). Sections for geochemistry were thawed and air dried in the laboratory. The colony received measured 70 cm in length and had a diameter of 26 mm at the base, which included a thick accumulation of calcite cortex (Fig. 3). Analyses of five tissue samples taken along the length of DFO-2002-con5 showed no difference in  $\delta^{13}\text{C}$ , within analytical error (Fig. 6). The exception was the tissue sample 20 cm from the top of the colony, which had a value 0.3 ‰ heavier than the rest.  $\delta^{15}\text{N}$  was slightly more variable, with values increasing steadily by 0.8 ‰ from the tip to the base of the colony. C:N varied by up to 2 among the different tissue samples. Stable isotope profiles (Fig. 7) of gorgonin layers were generated from two sections at the base of the colony, separated by a distance of 3 cm. C:N was not measured. Isotope

profiles were virtually identical among the two different sections ( $r = 0.69$  { $\delta^{13}\text{C}$ } and  $0.63$  { $\delta^{15}\text{N}$ };  $p < .0001$ ). Values of  $\delta^{13}\text{C}$  showed a convex upward trend, with heaviest values in the middle of the profile. Values of  $\delta^{15}\text{N}$  increased with age.

### **Comparison of modern and fossil specimens**

The two specimens from ca. 150 and 2000 yrs BP were compared to other corals collected alive from the NE Channel (Table 2). C:N ratios of these older specimens,  $3.4 \pm 0.1$  ( $n = 9$ ), were slightly higher than the modern ones,  $3.15 \pm 0.05$  ( $n = 260$ ). The fossil samples were heavier in  $\delta^{13}\text{C}$  by  $1.5 \text{‰}$  (Fig. 8). Part of this difference may be explained by the Suess effect, caused by the depletion of atmospheric  $^{13}\text{C}$  from the burning of fossil fuels, with subsequent depletion of oceanic dissolved inorganic carbon (DIC; Quay et al. 1992). The  $1.5 \text{‰}$  difference between the 150 yr old COHPS-2001-1 and the most recent samples from DFO-2002-con5 is consistent with the decrease in atmospheric  $\delta^{13}\text{C}$  between the mid 1800s and the present (Francey et al. 1999). The lighter values from ca. 1920, however, exceed the magnitude of the Suess effect. Therefore, there may be other oceanographic and/or trophic level changes affecting  $\delta^{13}\text{C}$  over shorter timescales. There was also a slight trend towards higher  $\delta^{15}\text{N}$  with age, with the two fossil specimens having similar values as the oldest layers from DFO-2002-con5 (Fig.8).

### **Radiocarbon profile**

Approximately one in every ten gorgonin rings isolated from colony DFO-2002-con5 (section A1), was analyzed for  $^{14}\text{C}$  (Fig. 9a). The sudden increase in  $\Delta^{14}\text{C}$  halfway

through the profile is caused by thermonuclear weapons testing beginning in the late 1950s (Nydal et al. 1998). The shape and amplitude (100 ‰) of the profile are identical to previous results measured in the carbonate shell of the long-lived ocean quahog, *Arctica islandica*, collected from a depth of 76 m on nearby Georges Bank (Fig. 9b; Weidman & Jones 1993).

### **$\delta^{15}\text{N}$ composition of plankton**

In order to assess the TL of *Primnoa resedaeformis* collected from the NE Channel (see below)  $\delta^{15}\text{N}$  at the base of the food web was assessed from measurements of  $\text{POM}_{\text{SUSP}}$ . Unfortunately, the NE Channel was not targeted for sampling in years 2000-2003 of the Ecosystems Monitoring Survey (Fig. 1). With the exception of the central shoals of Georges Bank,  $\delta^{15}\text{N}$  in surface water  $\text{POM}_{\text{SUSP}}$  was consistent throughout the entire region (4.1 +/- 1.2 ‰, n = 56; Fig.10). We therefore assume that this value is representative of  $\text{POM}_{\text{SUSP}}$  in waters overlying the NE Channel.

In August 2004, the NE Channel was occupied to collect  $\text{POM}_{\text{SUSP}}$  along a depth transect (Fig. 1). Below the euphotic zone  $\delta^{15}\text{N}$  increased rapidly to a maximum of 18.5 ‰ at 215 m depth (Fig. 11). While these data represent only one snapshot in time, they are consistent with earlier results reported for Wilkinson Basin, located farther inside the Gulf of Maine (Libes and Deuser 1988).

## DISCUSSION

### Trophic level

It has been suggested that deep-sea corals form their organic endoskeletons from sinking POM (POM<sub>SINK</sub>), based on modern  $\Delta^{14}\text{C}$  ( $> 0$  ‰) in the gorgonin fraction of *Gerardia* spp., *Paragorgia johnsoni* (Griffin & Druffel 1989) and *Primnoa resedaeformis* (Heikoop et al. 1998) collected in the NW Atlantic. This is based on measurements of dissolved organic carbon (DOC) that are typically around -400 ‰, and DIC around -50 ‰, at depths  $> 200$  m in this region (Bauer et al. 2002). Similarity of  $\Delta^{14}\text{C}$  profiles between *P. resedaeformis* (Fig. 9) and *Arctica islandica* (Weidman & Jones 1993) suggest that these two organisms synthesize their skeletons from the same pool of carbon. The carbon source for the carbonate shell of *A. islandica* is DIC in the shallow, well-mixed waters of Georges Bank. *P. resedaeformis*, therefore, must derive its gorgonin skeleton from carbon exported from the surface waters, via phytoplankton. These results support earlier work on deep-sea corals, but do not indicate whether *Primnoa* spp. feed upon sinking phytoplankton, zooplankton or other trophic intermediaries.

Further insight to the TL of *Primnoa* spp. is provided by  $\delta^{15}\text{N}$ . This is typically enriched in a consumer relative to its diet by an average enrichment factor of  $\Delta\delta^{15}\text{N} = 3.4$  ‰ (DeNiro & Epstein 1981, Minagawa & Wada 1984, Vander Zanden & Rasmussen 2001). The TL of *Primnoa* spp. corals may therefore be estimated by comparing our data with the isotopic signatures of other organisms of known TL (e.g. Vander Zanden et al. 1997, Polunin et al. 2001). We used primary consumers as the baseline, and calculated TL by the formula:  $\text{TL}_{\text{consumer}} = (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}}) / 3.4 + 2$  (Vander Zanden &

Rasmussen 2001). Wherever possible, we used the gorgonin, rather than tissue results, since these integrate seasonal and inter-annual isotopic variations occurring at the base of the food web. Our approach was to reconstruct regionally-specific TL models from literature data.

*Primnoa resedaeformis* from the NE Channel was compared with the TL model of Fry (1988), which was based on taxa collected from nearby Georges Bank. We added to this model isotopic data for POM<sub>SUSP</sub> (this study) POM<sub>SINK</sub> (Macko 1981) and size-fractionated zooplankton (Fry & Quinones 1994). Most of the invertebrates and fish reported in Fry (1988) and Fry & Quinones (1994) were collected within the 100 m isobath on Georges Bank, where  $\delta^{15}\text{N}$  of POM<sub>SUSP</sub> is 1.4 ‰ heavier than in surrounding waters (Fig. 10), probably as a result of greater use of regenerated ammonium on the Bank (Ostrom et al. 1997, Wu et al. 1999a). We assume that isotopic enrichment on Georges Bank is transmitted to higher trophic levels. This difference in  $\delta^{15}\text{N}$  equates to 0.4 trophic levels and must be accounted for in TL model output.

The NE Channel/Gulf of Maine  $\delta^{15}\text{N}$ -TL model is shown in Fig. 12. Data for the Georges Bank taxa were subtracted by 1.4 ‰. Herbivorous scallops were used for baseline  $\delta^{15}\text{N}$  (Fry 1988;  $6 - 1.4 = 4.6$  ‰). Among live-collected *Primnoa resedaeformis* from the NE Channel, the inter-colony average  $\delta^{15}\text{N}$  was  $10.0 \pm 0.3$  ‰ ( $n = 5$ ). This value is similar to the  $\delta^{15}\text{N}$  for large benthic isopods, large polychaetes, and planktivorous fish (Fig.12). The calculated TL is 3.6. This suggests that *P. resedaeformis* is primarily carnivorous. We have also observed that the polyps on *P. resedaeformis* point down, suggesting that these corals may also feed on resuspended meiofauna.



Another factor which may affect the TL estimate is isotopic modification of particulate matter in deep waters. Significant enrichment of  $\delta^{15}\text{N}$  below the euphotic zone (Fig. 11) rules out the possibility that *Primnoa resedaeformis* feeds on the highly degraded  $\text{POM}_{\text{SUSP}}$  encountered at depth (otherwise  $\delta^{15}\text{N}$  in *P. resedaeformis* would be much higher; Fig. 12).  $\text{POM}_{\text{SINK}}$  may also become isotopically enriched below the euphotic zone, although to a much lesser extent than  $\text{POM}_{\text{SUSP}}$  (Altabet et al. 1988, Altabet et al. 1991, Voss et al. 1996). We estimate that  $\text{POM}_{\text{SINK}}$  in the NE Channel has a  $\delta^{15}\text{N}$  signature of 6.5 ‰ based on sediment data (Macko 1981) and general similarity in  $\delta^{15}\text{N}$  between sediments and  $\text{POM}_{\text{SINK}}$  (Altabet & Francois 1994, Voss et al. 1996, Ostrom et al. 1997). Assuming  $\Delta\delta^{15}\text{N} = 3.4$ , *P. resedaeformis* could feed on  $\text{POM}_{\text{SINK}}$  as well as zooplankton (Fig. 12).

Heavier  $\delta^{15}\text{N}$  in *Primnoa willeyi* from the NE Pacific ( $12.8 \pm 0.6$  ‰,  $n = 5$ ), when compared to *Primnoa resedaeformis* from the NW Atlantic, may reflect either a difference at the base of the food web or higher TL. We constructed a TL model based on literature  $\delta^{15}\text{N}$  data from 2 inshore Bays near Juneau (Goering et al. 1990) and Prince William Sound, Alaska (Kline 1999; note: one of our specimens {Smith-51283} was collected in Prince William Sound). Baseline  $\delta^{15}\text{N}$  was set to 8 ‰, using the values reported for herbivorous copepods (*Neocalanus cristatus*; Kline 1999) and bivalves (Goering et al. 1990). Overlap in  $\delta^{15}\text{N}$  values among similar taxa from these two Alaskan bays, despite a separation of over 600 km, lends confidence that  $\delta^{15}\text{N}$  signatures are well conserved within the coastal NE Pacific ecosystem. We calculate a TL of about 3.4 for *P. willeyi*. Measurements of  $\text{POM}_{\text{SINK}}$  from off Vancouver Island ( $\delta^{15}\text{N} = 8\text{-}9$  ‰, Peña et al. 1999, Wu et al. 1999a) are also consistent with this fraction being a food source for *P.*

*willeyi*. Lighter  $\delta^{15}\text{N}$  in the sample from Atka Island (9.1 ‰) may be explained by low  $\delta^{15}\text{N}$  in offshore primary producers (Wu et al. 1997; see below).

It has been shown that coastal ecosystems often exhibit lower  $\Delta\delta^{15}\text{N}$  than the globally accepted value of 3.4 ‰ (Wu et al. 1997, Sherwood & Rose *in press*). To validate our TL estimates, we also looked at four taxa that were sampled in both the NE Pacific and NW Atlantic: euphausiids, bivalves, pollock, and sole. TL outputs for the two different ecosystems were statistically equal (matched-pairs t-test). Moreover, TL outputs for both ecosystems conform to expectations: bivalves (TL = 2); euphausiids (TL = 2.6); pollock (3.8); sole (3.5 to 3.8). Therefore, our use of  $\Delta\delta^{15}\text{N} = 3.4$  ‰ for both Georges Bank and coastal NE Pacific ecosystems does not appear to introduce bias in our model outputs.

In summary, isotopic data support the following three conclusions about the diet of *Primnoa* corals. (1) Presence of modern  $\Delta^{14}\text{C}$  in *Primnoa resedaeformis* rules out DOC as a significant carbon source to the gorgonin fraction of the skeleton. Measurements of  $\delta^{15}\text{N}$  suggest that (2) zooplankton and/or  $\text{POM}_{\text{SINK}}$  constitute the main diet of *P. resedaeformis* and *Primnoa willeyi*, and (3) the highly degraded fraction of  $\text{POM}_{\text{SUSP}}$  found at depth is not a significant food source. This is also supported by the finding that the dark, more gorgonin-rich portion of the annual ring couplets in *P. resedaeformis* co-incide with the timing of the spring/summer bloom of phytoplankton and zooplankton (Sherwood 2002).

Lack of isotopic data for the Sea of Japan and the South Pacific in the literature prevented a similar analysis of the TL of the remaining species. It is quite probable that

*Primnoa pacifica* and *Primnoa resedaeformis notialis* share a similar type of diet with *P. resedaeformis* and *P. willeyi*, since all the corals have similar-sized polyps.

As passive suspension feeders, octocorals feed opportunistically on a wide spectrum of plankton size classes, from nanoeukaryotes to zooplankton (Ribes et al. 1999, Orejas 2003, Ribes et al. 2003). Temperate and boreal asymbiotic species feed mainly on zooplankton and detrital POM in about equal proportion, with smaller plankton (<100  $\mu\text{m}$ ) accounting for < 10 % of energy demand (Ribes et al. 1999, Ribes et al. 2003). Among zooplankton, gorgonians ingest smaller, low-motility prey items (Coma et al. 1994, Rossi et al. 2004). Our isotopic data conform to this general pattern, with the exception that the highly degraded POM<sub>SUSP</sub> found at depth does not appear to be a significant food source. Heterogeneity of prey items may explain the differences in the reproducibility of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  from different sections of the same colony. It may be possible that different parts of the colony are more effective at capturing different sized prey items depending on localized current regimes (Coma et al. 1994). Differential feeding on prey size-classes could potentially alter  $\delta^{15}\text{N}$  signatures, due to strong trophic level fractionation of  $^{15}\text{N}$  (Fry & Quinones 1994). If this is true, then analyses of more sections per colony and more colonies per site are recommended to get the average  $\delta^{15}\text{N}$ . Since trophic level fractionation of  $^{13}\text{C}$  is much weaker (generally < 1 ‰; Vander Zanden & Rasmussen 2001) differential feeding should exert less influence on  $\delta^{13}\text{C}$ , thereby leading to greater isotopic reproducibility.

### **Surface-benthic coupling of isotopic signatures**

The overall isotopic signature of a food web is determined by bio-physical processes at the level of primary producers. These processes are myriad and complex, especially over shorter timescales. Phytoplankton  $\delta^{15}\text{N}$  mainly depends on the efficiency of nitrogen utilization (Nakatsuka et al. 1992, Altabet & Francois 1994, Wu et al. 1997, 1999a) and on the  $\delta^{15}\text{N}$  signature of the nitrogenous substrate (Ostrom et al. 1997, Altabet et al. 1999). Phytoplankton  $\delta^{13}\text{C}$  mainly depends on  $[\text{CO}_{2\text{aq}}]$  (Rau et al. 1992, Hoffman et al. 2000), growth rate (Nakatsuka et al. 1992, Hoffman et al. 2000) and cell geometry/plankton species composition (Popp et al. 1998, Fry & Wainright 1991), as well as the  $\delta^{13}\text{C}$  signature of the bicarbonate substrate (Cullen et al. 2001). As a result of these myriad factors, there are large isotopic differences between open ocean, slope water, and coastal ecosystems (Wu et al. 1997). Furthermore, different pathways of isotopic fractionation often lead to decoupling of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in new production (Ostrom et al. 1997, Wu et al. 1999a, 1999b). In Fig. 4b, our use of surface water AOU is not meant to imply control on isotopic fractionation, but to give some sense of the different surface productivity regimes where the corals lived. The lightest values were found in the South Pacific, located near a high nutrient-low chlorophyll (HNLC) domain, where despite high  $[\text{NO}_3]$  and  $[\text{CO}_{2\text{aq}}]$  primary production is limited by micronutrients such as iron. Similarly low values were observed in a specimen from Atka Island, in the Aleutian Islands, also located near an HNLC domain (Wu et al. 1999b). Heavier values were found in the slope water regions of the NW Atlantic and the Sea of Japan, where primary productivity is typically dominated by blooms of large, fast growing phytoplankton (Mousseau et al. 1996). These blooms lead to nutrient depletion, and heavier  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . The heaviest values were in corals from Alaska and British

Columbia, consistent with highest productivity rates in these coastal domains. These results demonstrate that isotopic signatures originating with primary producers are transmitted to, and preserved within, the organic endoskeletons of *Primnoa* spp. It is therefore not surprising that  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in *Primnoa* spp. are both so tightly correlated with AOU (Fig. 4b).

### **Preservation of original isotopic composition**

For isotopic trends from gorgonin to have any paleoceanographic utility, there must not be any diagenetic overprinting. In many of the fossil specimens donated to us by fishermen, the gorgonin appeared to be more susceptible to degradation than the inorganic calcite cortex fraction. On the broken axes of these dead colonies, the inner horny axis is often worn down in a smooth cup-shaped depression, while the cortex remains intact. Similarity in C:N,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  between modern and fossil specimens suggests that isotopic signatures are preserved from the time of original formation. This is also supported by similarity in amino acid abundances between modern and fossil specimens (O.A. Sherwood, unpublished data), since diagenesis often leads to the synthesis of microbial biomass with different amino acid and stable isotopic composition (Macko & Estep 1984). The degradation observed on fossil specimens appears to be the result of mechanical erosion, probably by the action of suspended sands, rather than organic diagenesis. This finding is consistent with gorgonin being one of the most chemically inert proteins known (Goldberg 1976). Over millennial timescales, therefore, isotopic abundances in *Primnoa* spp. are preserved, making these corals durable archives of paleoceanographic information.

## Paleoceanographic applications

Owing to little trophic level fractionation and excellent intra-colony reproducibility,  $\delta^{13}\text{C}$  time-series from *Primnoa* spp. could reliably track variations in surface processes. We have not yet assessed inter-colony reproducibility of isotopic profiles, as we are currently devising ways to construct accurate chronologies. From Figs. 5 and 7, it appears that two colonies of *Primnoa resedaeformis* from the NE Channel recorded a peak in  $\delta^{13}\text{C}$  around the mid-twentieth century, with several decade-scale oscillations. The causes of these variations are not clear; but there may be an important link with known changes in plankton community composition since the 1960s in this region (Sameoto 2001). On the other hand, evidence of the oceanic Suess effect on the  $\delta^{13}\text{C}$  composition of modern vs. fossil specimens (Fig. 8), and reconstruction of 20<sup>th</sup> century bomb radiocarbon (Fig. 10) are examples of isotopic variability in source materials recorded in these corals. Therefore, there is evidence that both biological processes (i.e. correlation of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  with AOU) and physical processes (changes in isotopic composition of bicarbonate substrate) are reflected in gorgonin isotopic content. Smaller regional studies with multiple colonies and good chronological control will be required to deconvolute these different factors. Useful information may also be extracted from  $\delta^{15}\text{N}$  profiles, provided that time-series variability is large relative to the intra- and inter-colony variability.

The annual nature of ring formation makes *Primnoa* spp. analogous to varved sediment cores, from which much useful paleoceanographic information has been retrieved (e.g. Tunnicliffe 2000). In similar fashion, annually-resolved isotope time-series have been generated from preserved animal remains, such as fish scales (Wainright et al.

1993) and whale baleen (Schell 2001). Long lifespans (at least 400 years, probably longer; Risk et al. 2002, Scott et al. 2005) lend to *Primnoa* spp. the advantages of both varved sediment cores (longer, *in situ* time-series) and preserved animal remains (widespread distribution, known TL). Isotopic reconstructions from *Primnoa* spp. could be useful in illustrating temporal variations in marine productivity, as well as tracking the relative importance of top-down vs. bottom-up influences over time (Schell 2001, Rau et al. 2003, Satterfield IV & Finney 2002). Oceanographic phenomena that may be recorded include changes in the position of water mass boundaries, upwelling strength, terrestrial nutrient inputs and atmospheric nutrient inputs.

Deep-sea corals could prove to be temporal and spatial recorders of the efficacy of the oceanic biological pump that transfers carbon dioxide from the atmosphere to the deep-ocean. By understanding natural processes that have affected the operation of this pump over century time scales we can better predict the effects of global change and potential engineered approaches such as iron fertilization on oceanic carbon sequestration. The widespread occurrence and diversity of deep-sea corals is only now being fully appreciated. As more deep-sea corals are discovered in important oceanographic regions the applicability of this potential paleoceanographic archive is likely to increase.

## CONCLUSIONS

1. Measurements of  $\Delta^{14}\text{C}$  and  $\delta^{15}\text{N}$  indicate that *Primnoa resedaeformis* and *Primnoa willeyi* have a TL of about 3.5.  $\text{POM}_{\text{SINK}}$  and zooplankton appear to constitute the bulk of the diet, whereas DOC and  $\text{POM}_{\text{SUSP}}$  are not consumed. The TL for *Primnoa pacifica* and

*Primnoa resedaeformis notialis* could not be determined, but it is likely that these species feed at a similar TL, based on similar sized polyps.

**2.** Average  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  compositions of the gorgonin fraction were strongly correlated with each other, and with surface water AOU. This demonstrates strong coupling between surface bio-physical processes and stable isotopic compositions in *Primnoa* spp.

**3.** Isotopic profiles from annual gorgonin rings showed excellent intra-colony reproducibility for  $\delta^{13}\text{C}$ , while  $\delta^{15}\text{N}$  became more irreproducible with greater separation of axial sections along the length of the colony. The latter result may arise from differential feeding upon different sized prey items, depending on localized current regimes; however, more work is needed to address this issue.

**4.** The utility of *Primnoa* spp. as archives of surface water processes was demonstrated by reconstruction of twentieth century bomb radiocarbon.

**5.** Similarity in C:N,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  between modern and fossil specimens demonstrates a lack of organic diagenesis in the tough gorgonin fraction. Isotopic signatures from the time of formation are therefore preserved over millennial timescales, making these corals excellent candidates for retrospective studies of the surface marine environment.



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**Table 1:** Summary of *Primnoa* samples.

Sample	Species	Location	Year collected	Lat	Lon	Depth
		<b>NW ATLANTIC</b>				
ROPOS 637052	<i>P. resedaeformis</i> (Gunnerus)	NE Channel	2001	42.048°N	65.577°W	475
ROPOS 639009	<i>P. resedaeformis</i> (Gunnerus)	NE Channel	2001	41.998°N	65.648°W	410
HUD-2000-020-VG2	<i>P. resedaeformis</i> (Gunnerus)	NE Channel	2000	42.047°N	65.610°W	331
HUD-2001-055-VG-15	<i>P. resedaeformis</i> (Gunnerus)	NE Channel	2001	42.021°N	65.682°W	321
DFO-2002-con5	<i>P. resedaeformis</i> (Gunnerus)	NE Channel	2002	42.0°N <sup>d</sup>	-65.6°W <sup>d</sup>	250-500
COHPS-2001-1 <sup>a</sup>	<i>P. resedaeformis</i> (Gunnerus)	NE Channel	2001	42.0°N <sup>d</sup>	-65.6°W <sup>d</sup>	250-500
Fossil-95 <sup>b</sup>	<i>P. resedaeformis</i> (Gunnerus)	NE Channel	1995	42.0°N <sup>d</sup>	-65.6°W <sup>d</sup>	250-500
Smith-54269	<i>P. resedaeformis</i> (Gunnerus)	East of Virginia Beach	1974	37.060°N	74.410°W	237-385
		<b>NE PACIFIC</b>				
QC-98	<i>P. willeyi</i> (Hickson)	East of Queen Charlotte Islands	1998	54.386°N	132.786°W	378
KIS-02	<i>P. willeyi</i> (Hickson)	Knight Inlet sill, British Columbia	2002	50.679°N	126.000°W	65
Smith-51283 <sup>c</sup>	<i>P. pacifica</i> (Kinoshita)	Prince William Sound, Alaska	1941	61.034°N	146.714°W	64
Smith-52199	<i>P. willeyi</i> (Hickson)	Chatham Sound, British Columbia	1960	54.5°N <sup>d</sup>	130.5°W <sup>d</sup>	n/a
Smith-1010257	<i>P. willeyi</i> (Hickson)	Atka Island, Alaska	2002	51.9°N <sup>d</sup>	174.1°W <sup>d</sup>	213-220
Smith-1010785	<i>P. willeyi</i> (Hickson)	South of Chirikof Island, Alaska	2000	55.5°N <sup>d</sup>	155.5°W <sup>d</sup>	235
		<b>SEAOJ JAPAN</b>				
SOJ-03	<i>P. pacifica</i> (Kinoshita)	South of Vladivostok, Russia	2003	42.482°N	132.572°E	913
Smith-56993 <sup>c</sup>	<i>P. pacifica</i> (Kinoshita)	West of Hokkaido, Japan	1906	43.000°N	140.175°E	713-783
<b>S PACIFIC – SOUTHERN OCEAN SCETOR</b>						
Smith-58171 <sup>c</sup>	<i>P. resedaeformis notialis</i> (Bayer)	S. Pacific Seamount	1964	54.833°S	129.833°W	604
Smith-87624 <sup>c</sup>	<i>P. resedaeformis notialis</i> (Bayer)	S. Pacific Seamount	1964	54.817°S	119.800°W	549

<sup>a</sup> Fossil specimen, ca. 150 yrs old based on <sup>210</sup>Pb dating<sup>b</sup> Fossil specimen, ca. 2000 yrs old based on U-Th dating (Scott et al. 2005)<sup>c</sup> preserved in ethanol<sup>d</sup> Exact co-ordinates unknown; these are general co-ordinates for the location reported

**Table 2:** Summary of stable isotope and C:N data (Mean +/- 1 $\sigma$ ).

Sample	TISSUE					GORGONIN				
	n	C:N	$\delta^{13}\text{C}$	$\delta^{13}\text{C}'$	$\delta^{15}\text{N}$	n	C:N	$\delta^{13}\text{C}$	$\delta^{13}\text{C}'$	$\delta^{15}\text{N}$
<b>NW ATLANTIC</b>										
ROPOS 637052	3	7.70 +/- .47	-23.68 +/- .06	-21.50	10.22 +/- .12	16	-	-19.15 +/- .28	-20.3 <sup>c</sup>	9.74 +/- .15
ROPOS 639009	3	7.45 +/- .31	-23.92 +/- .20	-21.82	10.12 +/- .05	26	3.17 +/- .04	-19.13 +/- .49	-20.34	9.95 +/- .47
HUD 2000-020-VG2	-	-	-	-	-	12	3.17 +/- .05	-19.38 +/- .27	-20.59	9.50 +/- .51
HUD2001-055-VG-15	-	-	-	-	-	107	3.15 +/- .03	-19.01 +/- .74	-20.25	10.13 +/- .56
DFO-2002-con5	5	7.25 +/- .80	-23.87 +/- .30	-21.84	10.58 +/- .31	99	-	-19.03 +/- .55	-20.18 <sup>c</sup>	10.28 +/- .4
COHPS2001-1	-	-	-	-	-	21 <sup>b</sup>	3.41 +/- .10	-17.79 +/- .53	-18.59	10.86 +/- .47
Fossil-95	-	-	-	-	-	6	3.46 +/- .07	-18.29 +/- .48	-19.01	10.99 +/- .45
Smith-54269 <sup>a</sup>	4	-	-20.65 +/- .34	-	-	1	-	-18.35	-19.50 <sup>c</sup>	11.8
<b>NE PACIFIC</b>										
QC-98	3	7.67 +/- .57	-21.17 +/- .20	-19.00	13.26 +/- .13	3	3.22 +/- .04	-17.93 +/- .16	-19.04	12.82 +/- .20
KIS-02	1	5.73	-19.42	-18.05	13.80	8	3.26 +/- .06	-16.08 +/- .34	-17.13	12.26 +/- .33
Smith-51283 <sup>a</sup>	5	-	-16.50 +/- .38	-	-	2	-	-16.17 +/- .39	-17.32 <sup>c</sup>	13.8
Smith-52199	1	4.06	-18.24	-18.17	12.53	-	-	-	-	-
Smith-1010257	4	6.89 +/- .43	-23.77 +/- .04	-21.87	9.09 +/- .22	-	-	-	-	-
Smith-1010785	3	6.22 +/- .23	-19.49 +/- .15	-17.86	12.75 +/- .18	-	-	-	-	-
<b>SEA OF JAPAN</b>										
SOJ-03	3	4.87 +/- .03	-22.45 +/- .11	-21.64	12.91 +/- .16	2	3.22 +/- .02	-19.46 +/- .11	-20.58	10.45 +/- .37
Smith-56993	3	4.52 +/- .05	-21.24 +/- .38	-20.72	10.67 +/- .09	-	-	-	-	-
<b>SOUTH PACIFIC - SOUTHERN OCEAN SECTOR</b>										
Smith-58171	3	4.12 +/- .01	-22.05 +/- .30	-21.91	7.76 +/- .12	3	-	-	-	-
Smith-87624 <sup>a</sup>	3	-	-21.14 +/- .57	-	-	2	-	-20.41 +/- .45	-21.56 <sup>c</sup>	7.8

<sup>a</sup> Isotopic analyses performed at University of New Mexico; all others at GEOTOP<sup>b</sup> Only 3 samples were analyzed for C:N<sup>c</sup> assumes a C:N ratio of 3.2



## FIGURE CAPTIONS

**Fig. 1:** Map of the Gulf of Maine region, NW Atlantic Ocean. Colonies of *Primnoa resedaeformis* were collected from the NE Channel. Symbols show locations of water samples for analysis of POM<sub>SUSP</sub>.

**Fig. 2:** Colonies of *Primnoa resedaeformis* collected from the NE Channel: (a) HUD-2001-055-VG15 (tissue missing) and (b) DFO-2002-con5 (tissue present). Sections for isotopic time-series profiles are indicated by boxes, tissue samples are indicated by arrows. Ruler for scale is 15 cm.

**Fig. 3:** Section A5 from DFO-2002-con5, photographed under ultraviolet light. White portion towards the outside is the inorganic calcite cortex. Darker layers towards middle are annual gorgonin rings isolated for chemical analyses. Specimen is approx. 75 yrs old, based on growth ring counts. Bar for scale is 0.5 cm.

**Fig. 4:** (a) Plot of average  $\delta^{15}\text{N}$  vs.  $\delta^{13}\text{C}'$  (lipid-normalized  $\delta^{13}\text{C}$ ) from the gorgonin fraction of different *Primnoa* spp. colonies. (b) Same data, plotted against Apparent Oxygen Utilization in surface water. Note, where gorgonin was not measured, the tissue isotopic values were plotted instead.

**Fig. 5:** Isotopic and C:N profiles from three different sections of HUD-2001-055-VG15 (see Fig. 2a for location of sections along colony axis). Time-span of profiles, estimated from ring counts, is approx. 1965 to 2000).

**Fig. 6:** Isotopic and C:N data from the tissue fraction of colony DFO-2002-con5 (see Fig. 2b for sample locations along colony axis). Error bars are  $1\sigma$ .

**Fig. 7:** Isotopic profiles from two different sections of colony DFO-2002-con5 (see Fig. 2b for locations along colony axis). Time-span of profiles, estimated from ring counts, is approximately 1920s to 1990s.

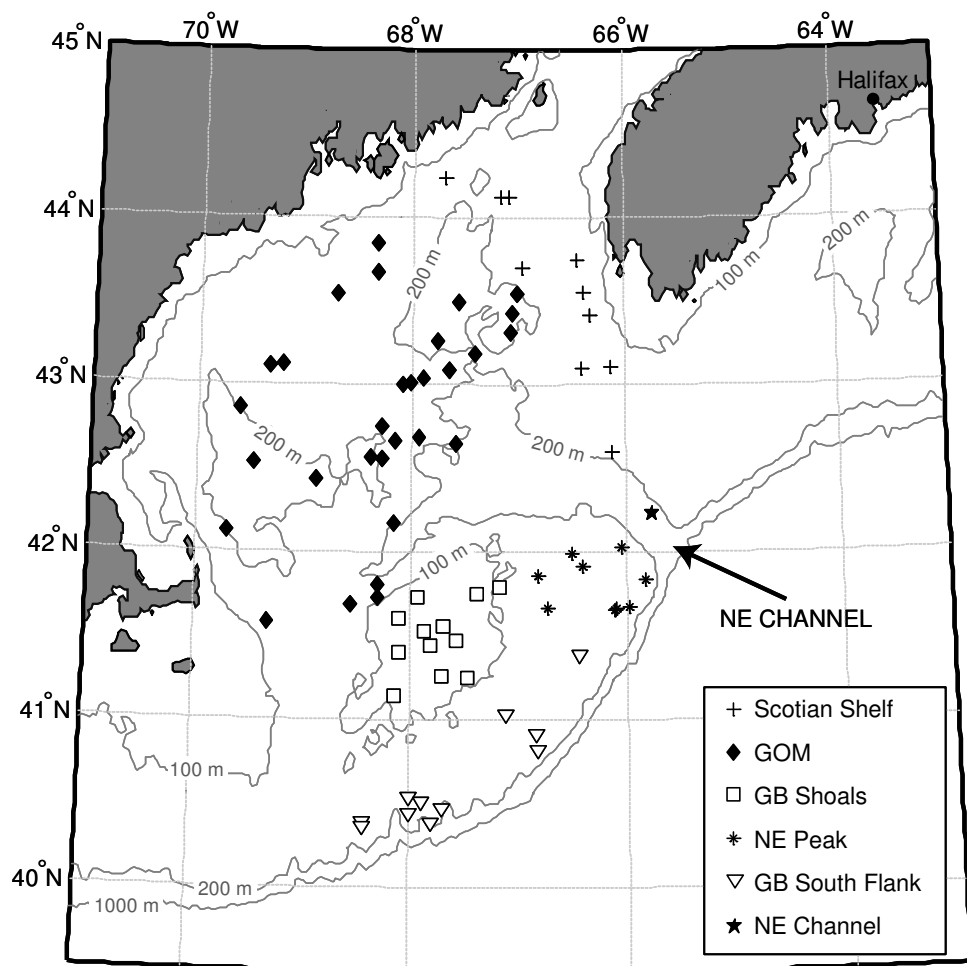
**Fig. 8:** Isotope profiles from a modern and two “fossil” colonies of *Primnoa resedaeformis* collected from the NE Channel. Age assignments (in calendar years) are based on ring counts (DFO-2002-con5),  $^{210}\text{Pb}$  (COHPS-2001-1) and uranium-series dating (Fossil-95).

**Fig. 9:** Radiocarbon profiles from a) *Primnoa resedaeformis* (DFO-2002-con5 section A1) collected from approx. 400 m in the NE Channel (note: chronology is approximate only) and b) *Arctica islandica* collected from 75 m on Georges Bank. Mid-20<sup>th</sup>-century peak corresponds to pulse in bomb radiocarbon in ocean surface water in late 1960s. Error bars are  $1\sigma$ .

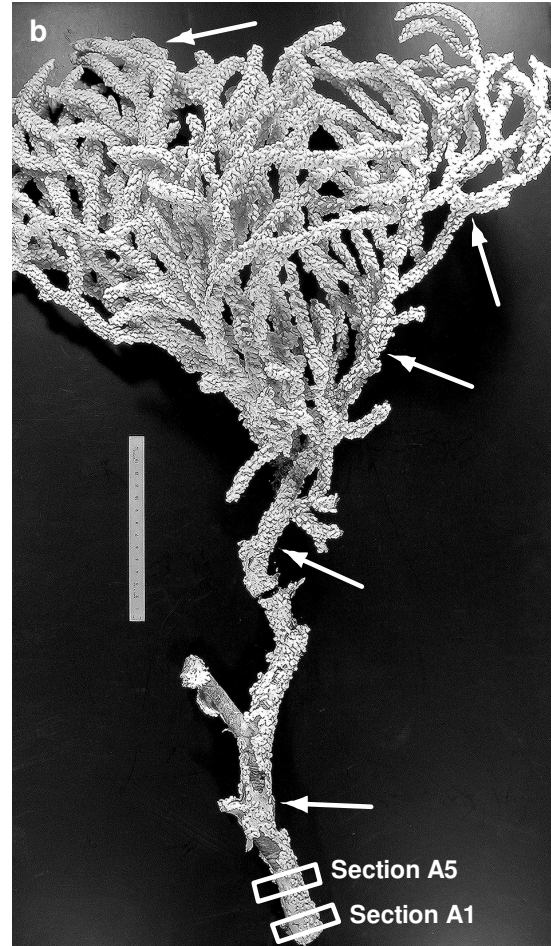
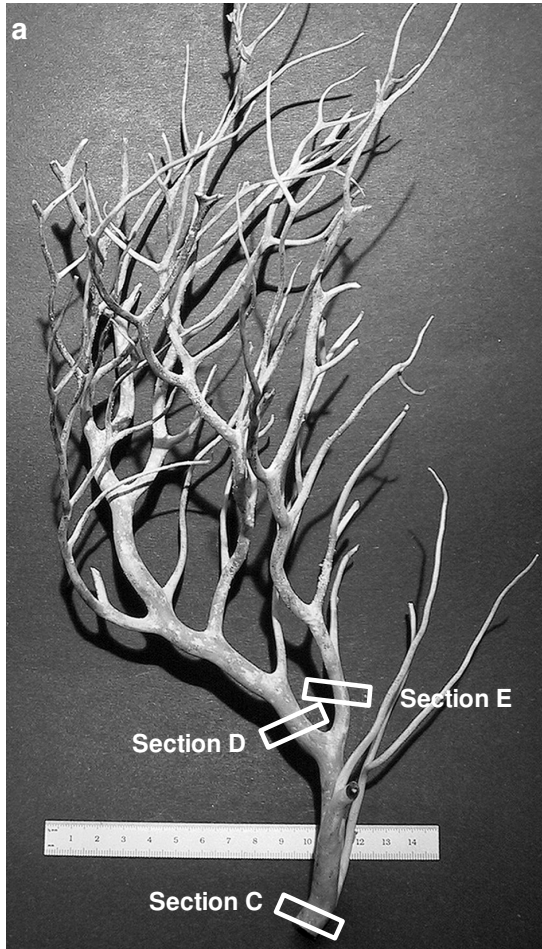
**Fig. 10:** Average ( $\pm 1\sigma$ )  $\delta^{15}\text{N}$  of  $\text{POM}_{\text{SUSP}}$  in surface waters of the different areas in the Gulf of Maine/Georges Bank region. Site designations correspond to Fig. 1.

**Fig. 11:** Depth profile of  $\delta^{15}\text{N}$   $\text{POM}_{\text{SUSP}}$  from NE Channel (this study, see Fig. 1) and from Wilkinson Basin inside the Gulf of Maine (Libes & Deuser 1988).

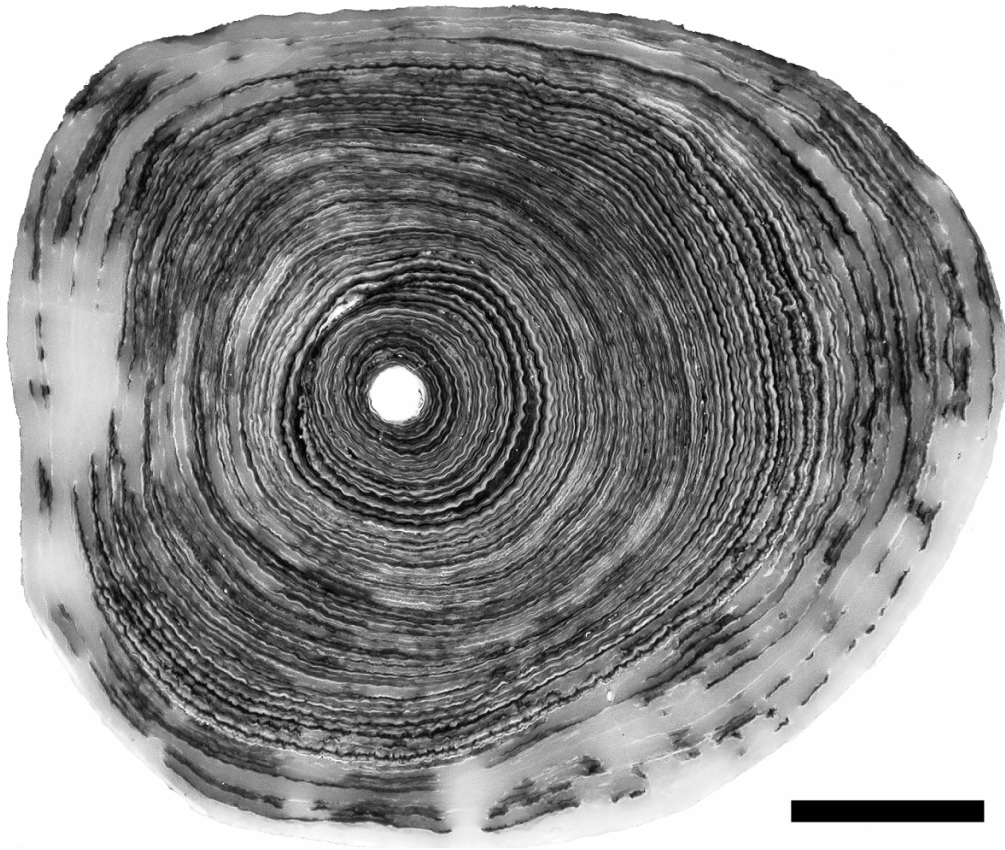
**Fig. 12:** TL- $\delta^{15}\text{N}$  model for the NE Channel/Gulf of Maine region. Open symbols representing Georges Bank taxa (data from Fry 1988 and Fry & Quinones 1994) subtracted by 1.4 ‰ to account for higher  $\delta^{15}\text{N}$  on Georges Bank (see text for explanation). Additional data (closed symbols) show surface  $\text{POM}_{\text{SUSP}}$  (this study), deep  $\text{POM}_{\text{SUSP}}$  (average between data from this study and Libes and Deuser 1988) and  $\text{POM}_{\text{SINK}}$  (based on sedimentary  $\delta^{15}\text{N}$  data from Macko 1981). Error bars (for closed symbols only) are  $1\sigma$ . TL designations are based on average composition of scallops (TL 2) and  $\Delta\delta^{15}\text{N} = 3.4$  ‰.



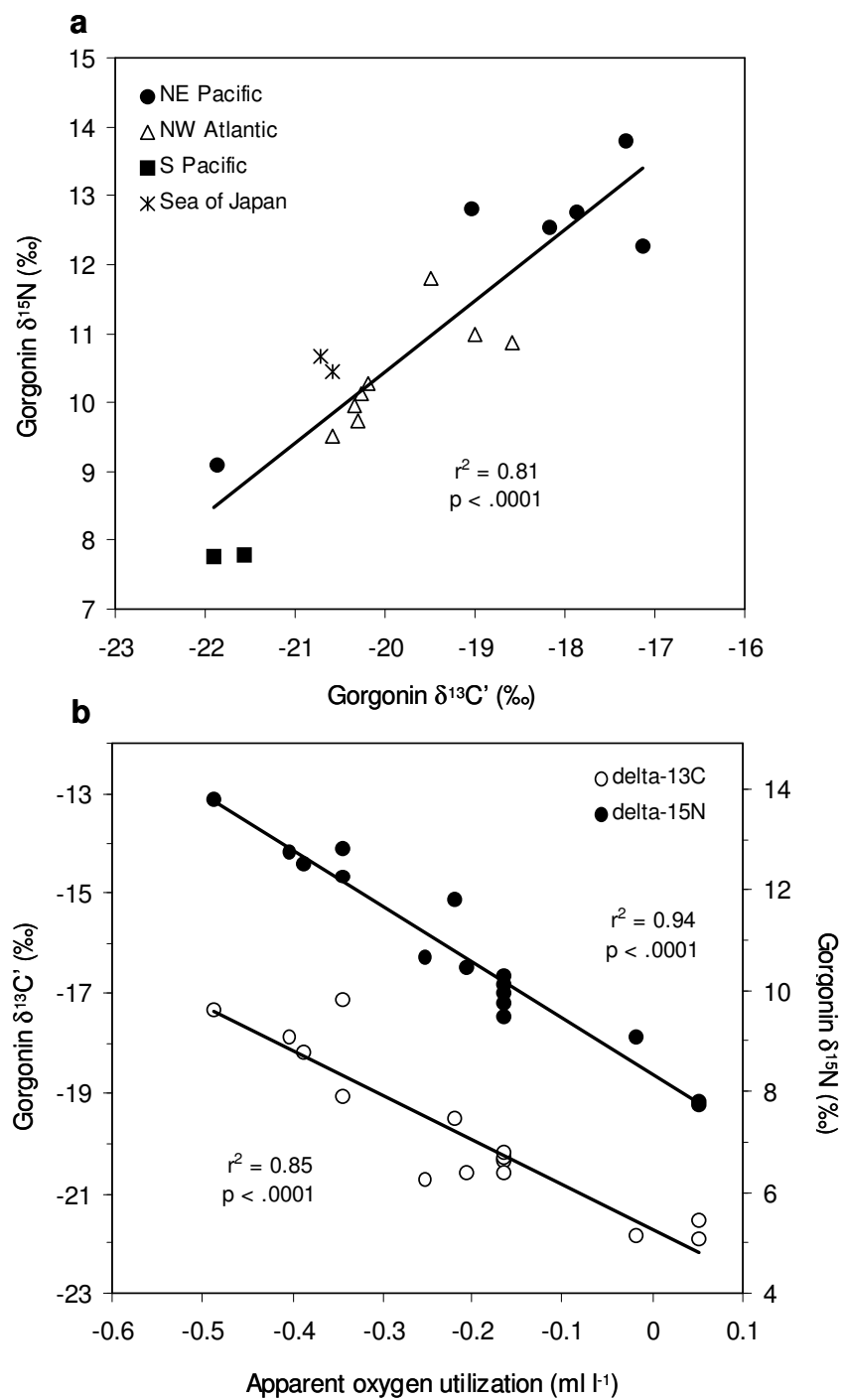
**Sherwood et al.**  
**Fig. 1**



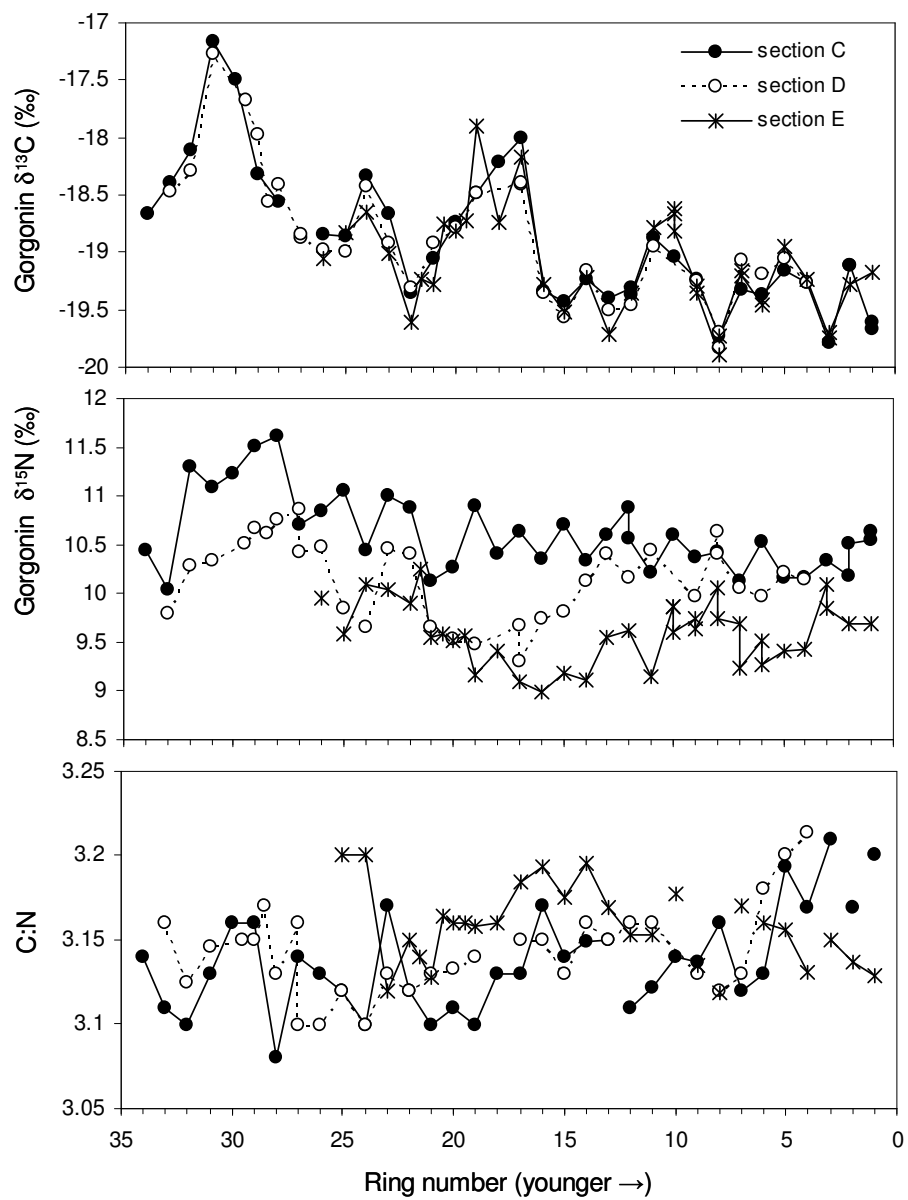
**Sherwood et al.**  
**Fig. 2**



**Sherwood et al.**  
**Fig. 3**

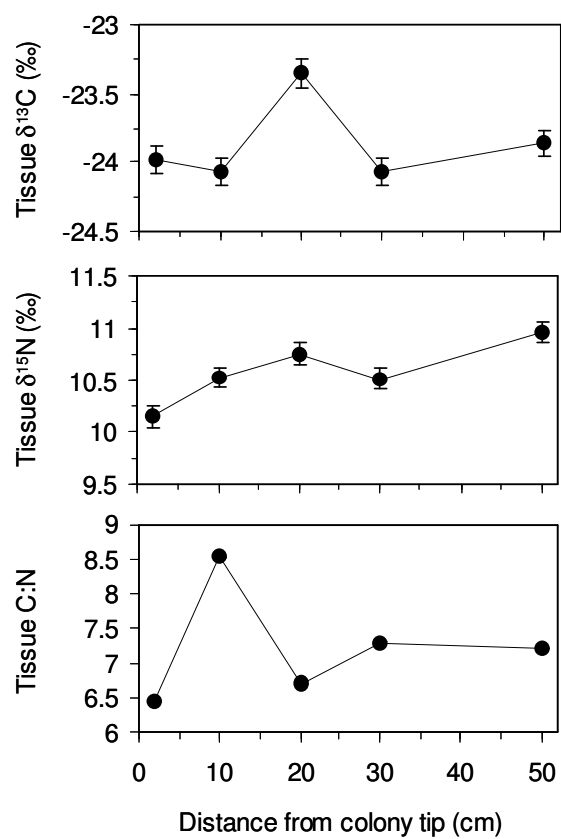


Sherwood et al.  
Fig. 4

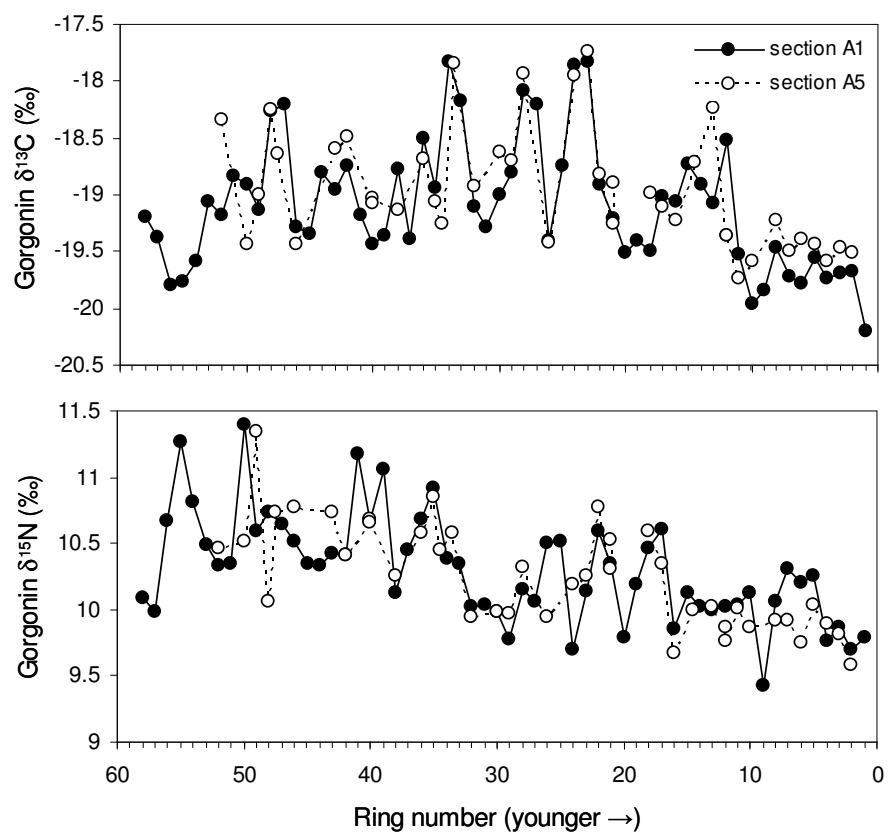


Sherwood et al.  
Fig. 5

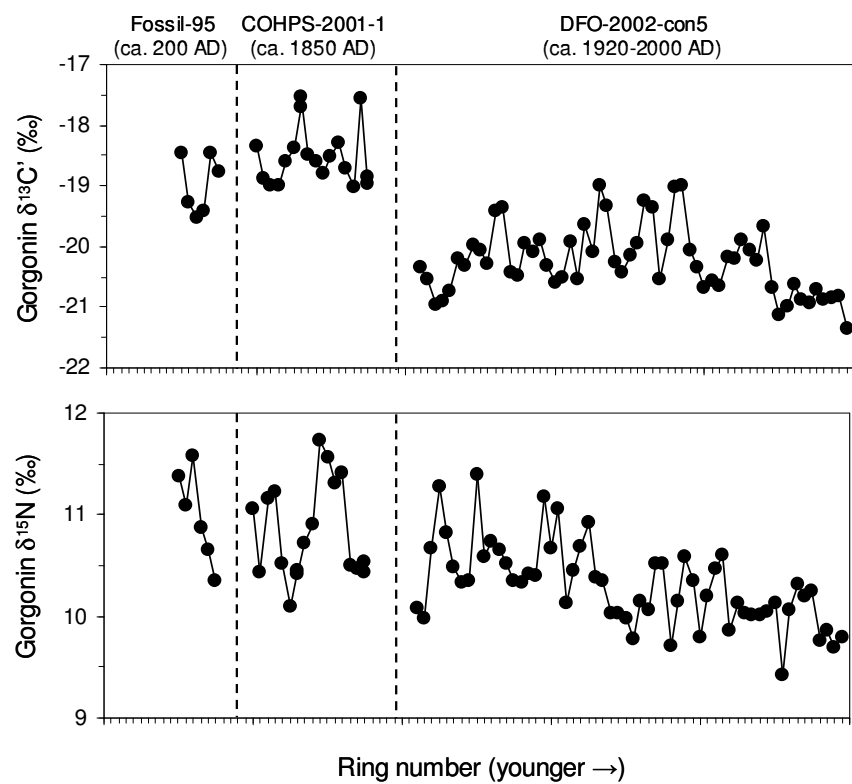




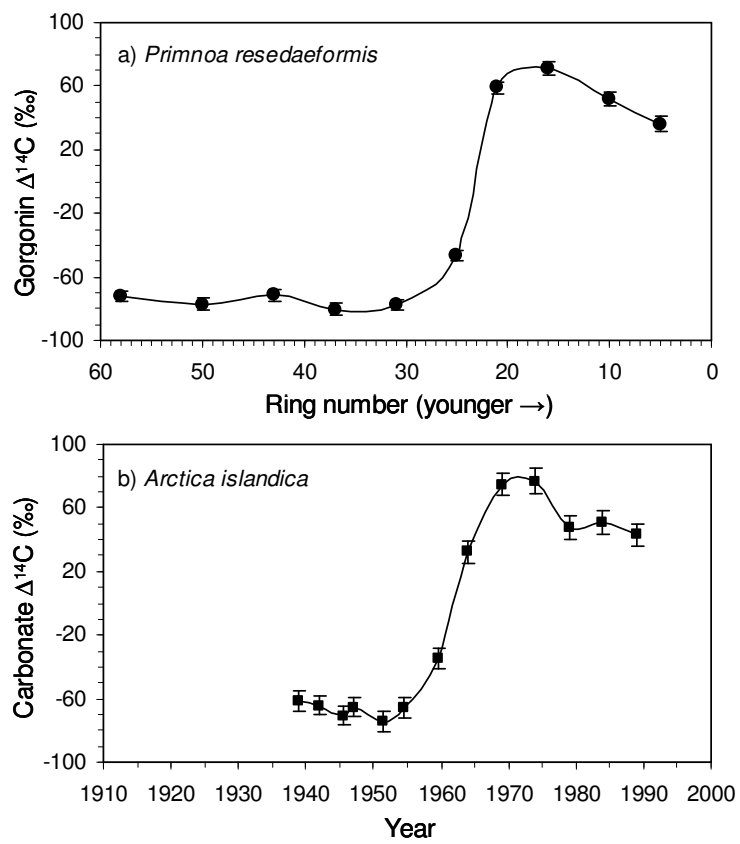
Sherwood et al.  
Fig. 6



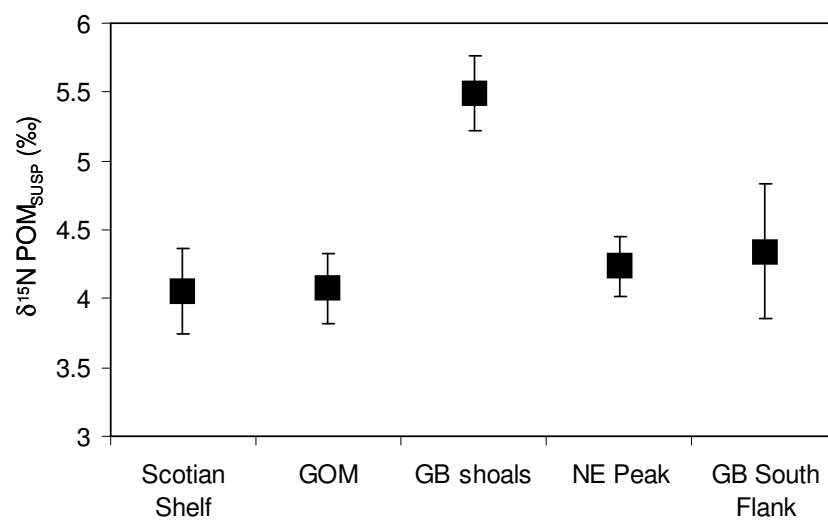
**Sherwood et al.**  
**Fig. 7**



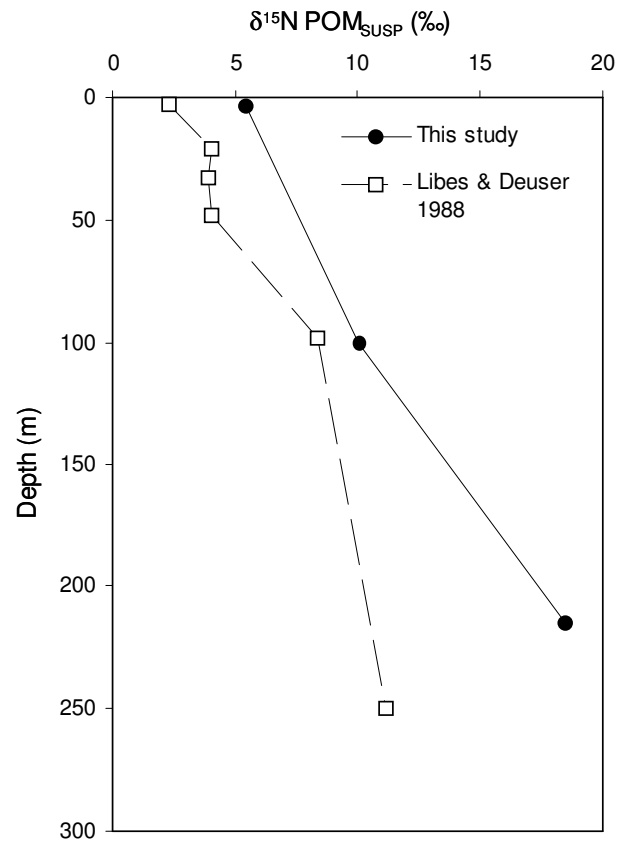
**Sherwood et al.**  
**Fig. 8**



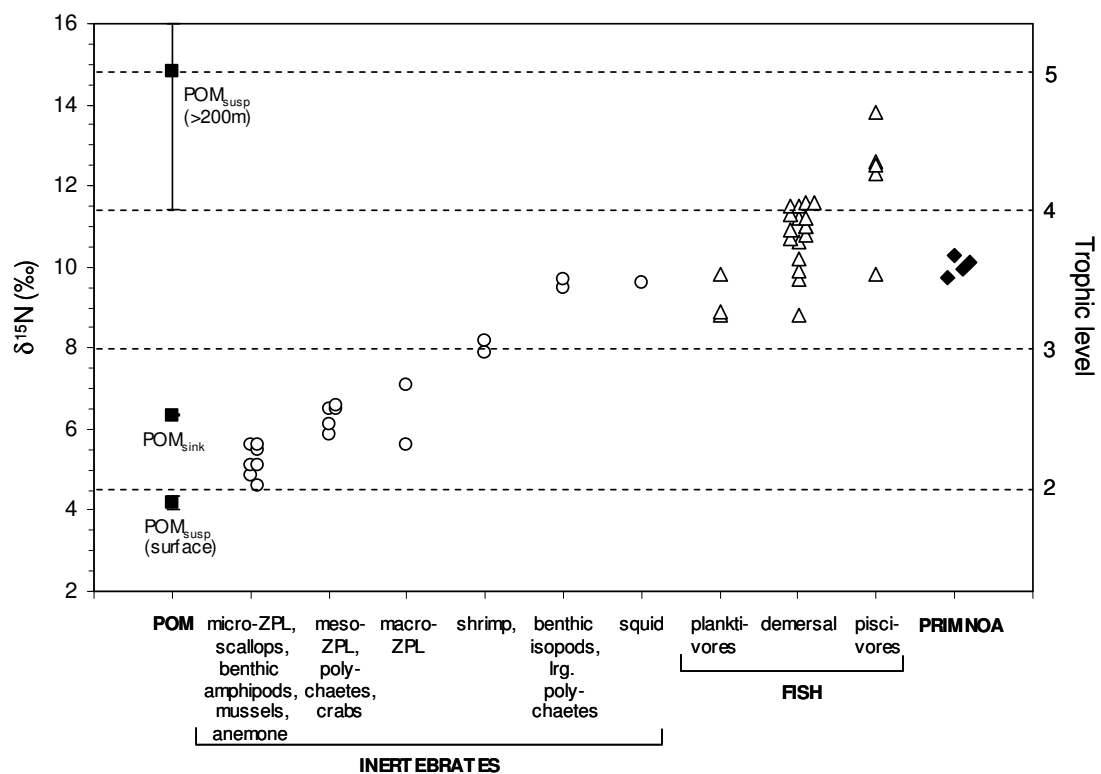
Sherwood et al.  
Fig. 9



**Sherwood et al.**  
**Fig. 10**



Sherwood et al.  
Fig. 11



Sherwood et al.  
Fig. 12